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TRANSFER OF *ASTER KINGII* TO *TONESTUS* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Aster kingii is not accommodated in *Machaeranthera* or *Xylorhiza*, the only genera outside of *Aster* with which it has been formally aligned. Studies have returned it to *Aster*, its original position, but it has not been accepted even there in recent taxonomic overviews. Placements alternative to *Aster* have not been suggested by previous workers. Although it is white rayed, the species is transferred here to the primarily yellow rayed genus *Tonestus*, where it is hypothesized to be most closely related to the rayless *T. aberrans*. The new combinations required are **T. kingii** (D.C. Eaton) Nesom and **T. kingii** var. **barnebyana** (Welsh & Goodrich) Nesom.

KEY WORDS: *Tonestus, Aster, Machaeranthera*, Asteraceae, Astereae

Aster kingii D.C. Eaton, a species restricted to the Wasatch and Canyon Mountains of central to north central Utah, has been unsettled in its systematic placement in the last 35 years. It was accepted by earlier North American taxonomists within the bounds of the large and variable genus *Aster* L., but Cronquist & Keck (1957) excluded the species from *Aster* and placed it in their expanded version of *Machaeranthera* Nees (within sect. *Xylorhiza* [Nutt.] Cronq. & Keck series *Integrifoliae* Cronq. & Keck). These authors noted (p. 233) that "The monocephalous montane true perennial '*Aster*' *kingii* D.C. Eaton is suggestive of *Xylorhiza glabriuscula*, but the involucre is that of *Machaeranthera*, and the plant blooms in late summer like other *Machaeranantherae*."

The species of *Machaeranthera* sect. *Xylorhiza* are now treated as the genus *Xylorhiza* Nutt., mostly following the monograph by Watson (1977). *Aster kingii*, however, was noted by Watson (1978, p. 209) to be "phenologically, ecologically, morphologically, and chromosomally anomalous ..." within *Xylorhiza*, while he observed resemblances in various features between *A. kingii*

and *A. alpigenus* (Torr. & Gray) A. Gray (in habit), *A. conspicuus* Lindl. (in phyllary morphology), and *A. integrifolius* Nutt. (in vestiture), although in 1977 he had suggested that it might prove to belong to *Machaeranthera* sect. *Machaeranthera*. Welsh (1983) accepted Watson's later point of view and treated the species as *Aster*, transferring a varietal taxon (var. *barnebyana*, see below) named in *Machaeranthera* to a position in *Aster*. In a taxonomic conspectus of the genus *Machaeranthera*, Hartman (1990) also excluded *A. kingii*, leaving it in *Aster*, although he did not provide a commentary regarding its possible affinities there. In contrast, recent taxonomic and phyletic overviews of the genus *Aster* (Jones 1980; Semple & Brouillet 1980; Jones & Young 1983) did not provide a position for *A. kingii* or even a mention of it in any context, although Dr. Jones (pers. comm.) now accepts it as a species of *Aster* sect. *Oreostemma* (E. Greene) Peck.

The chromosome number of *Aster kingii* ($n = 9$ pairs; Watson 1978, for var. *kingii*; Sanderson *et al.* 1984, for var. *barnebyana*) contrasts with all species of *Xylorhiza* ($x = 6$) as well as those of *Machaeranthera* ($x = 4, 5$). Species in groups of *Aster* hypothesized by Jones & Young (1983) to be primitive within the genus have a base chromosome number of $x = 9$, and this is presumably the area where *A. kingii* would find its closest phyletic affinities were it established that it lies within that lineage.

Aster kingii might be left in a broadly conceived *Aster* but its placement there would remain anomalous, as even in that heterogeneous group there are no species to which it can be unequivocally related. The three species of sect. *Oreostemma* appear to be relatively homogeneous, the plants all with nine pairs of chromosomes, producing a taproot and short branched caudex, strictly monocephalous stems, stems and leaves eglandular or with few, short stipitate glands, entire, linear leaves with three parallel veins, and flattened pappus bristles. The phyllaries in subg. *Oreostemma* are slightly keeled but the midvein near the phyllary base is usually sunken rather than raised. None of these features except the chromosome number and taproot are matched in *A. kingii*.

On the other hand, *Aster kingii* clearly is similar in a suite of features to the group of species recently consolidated as the genus *Tonestus* A. Nels. (Nesom & Morgan 1990): habitats rocky and at high altitudes, plants rhizomatous or taprooted with ascending, woody caudex branches, leaves obovate, reticulate veined, and coarsely toothed, the basal persistent, the cauline continuing to immediately below the heads, outer phyllaries foliaceous, at least the inner with a raised keel beginning at the phyllary base and with distinctively extended, foliaceous apices, and achenes strigose, long, narrow, and multinerved, with a nearly symmetrical carpopodium and with a single series of pappus bristles terete to the very base and more or less even in length. The vestiture, particularly of the stems, is composed of very long (up to 0.7 mm), vitreous, biseriate, gland tipped trichomes (Type C trichomes, see Nesom 1976). Type

C trichomes are ubiquitous throughout the tribe, but such distinctively long ones are rare among American Astereae, where to my knowledge, outside of *Tonestus* they occur only in *Aster integrifolius* and *A. modestus* Lindl., *Xylorhiza wrightii* (A. Gray) E. Greene, and a few species of *Solidago* L. In other features, *A. integrifolius* is securely positioned within *Aster* but *A. modestus* is anomalous and more difficult to place; neither could be considered to be closely related to *Tonestus*. *Xylorhiza* is more similar to *Machaeranthera* Nees, and *Solidago* has been shown by DNA studies to be closely related to *Tonestus* (see Nesom *et al.* 1990 for a summary). Two species within *Tonestus* are atypical in their vestiture – *T. microcephalus* (Cronq.) Nesom & Morgan is glabrous to glabrate and *T. pygmaeus* (Torr. & Gray) A. Nels. usually is eglandular – but they belong in the genus on the basis of overall morphology. The type species, *T. lyallii* (A. Gray) A. Nels., which is apparently one of the most specialized in the genus with its calvous achenes and (at least in some plants) somewhat flattened pappus bristles, also produces the very long glandular trichomes.

Among the species of *Tonestus, T. aberrans* (A. Nels.) Nesom & Morgan is most similar to *Aster kingii*. Indeed, as a pair the two are somewhat set apart from the rest of the genus in their toothed leaves often with spinulose teeth, narrowly lanceolate-attenuate and apically spreading or reflexed phyllaries, style appendages with more widely arranged sweeping hairs, and purplish disc corolla lobes. *Tonestus aberrans*, however, has leaves more predominately cauline and consistently produces multi-headed capitulescences in contrast to the normally monocephalous stems of *A. kingii*, although the latter occasionally may produce up to five heads in a loose corymb (*fide* Welsh 1983). Further, the leaves of *T. aberrans* are glandular pubescent while those of *A. kingii* are glabrous or glabrate, and the phyllaries of *T. aberrans* are distinctly graduated in length, while those of *A. kingii* are somewhat variable in this respect but also tend to be graduated.

A conspicuous feature that has deterred consideration of *Aster kingii* as a member of any yellow rayed genus is its white ray color. The complete absence of rays, however, in three species of *Tonestus* (*T. aberrans, T. graniticus* [Tiehm & Shultz] Nesom & Morgan, and *T. alpinus* [Anderson & Goodrich] Nesom & Morgan) has not previously prevented botanists from recognizing their close relationship with the yellow rayed species (Anderson 1980; Tiehm & Shultz 1985). If the hypothesis of close relationship regarding *A. kingii* and *T. aberrans* is correct, the purplish pigments in the disc corolla lobes of *T. aberrans* are perhaps unmasked by a reduced amount of yellow pigment. *Tonestus graniticus* has strongly graduated phyllaries and is probably closely related to *T. aberrans*. On the basis of its broader phyllaries of nearly even length, *T. alpinus* is probably most closely related to *T. eximius* (H.M. Hall) A. Nels. & Macbr. and *T. peirsonii* (Keck) Nesom & Morgan.

A second disparity, at first sight, between *Aster kingii* and the species of *Tonestus* might be perceived in the relatively well defined taproot of the for-

mer. All but two species of *Tonestus*, however, produce woody, ascending caudex branches apparently arising from a single axis, although the latter is usually broken off of herbarium specimens, probably because of the difficulty in extracting them from their crevice habitats. *Tonestus pygmaeus*, however, is clearly taprooted with a multicipital crown and foreshortened caudex branches and is nearly identical in habit to *A. kingii; T. microcephalus*, and *T. peirsonii* are taprooted with longer caudex branches. The relatively slender, more diffuse rhizomes of *T. lyallii* and *T. eximius* do not arise from a central axis and in this respect are unusual in the genus. Within *Tonestus*, taproots have perhaps developed in the manner hypothesized by Welsh (1983), but a more detailed analysis of the generic phylogeny would be required to establish this with certainty. In any case, other genera of Astereae accommodate both taprooted and rhizomatous species (e.g., *Chrysopsis* [Nutt.] Ell., *Erigeron* L., *Grindelia* Willd., *Gutierrezia* Lag., *Machaeranthera* Nees, *Noticastrum* DC. and numerous others). Within *Aster*, *A. subulatus* Michx. of subg. *Oxytripolium* (DC.) Torr. & Gray is a taprooted annual, its closest relatives rhizomatous. The species of *Aster* subg. *Ianthe* (Torr. & Gray) A. Gray (or the genus *Ionactis* E. Greene) are variable in their production of short, woody rhizomes, caudex branches, and taproots (Nesom & Leary, submitted). The remaining species of *Aster* sensu lato are somewhat more uniform in their rhizomatous bases, although the cormoid rhizomes of subg. *Virgulus* (Raf.) A. Jones are distinctive.

In summary, *Aster kingii* shares with species of *Tonestus* a significant number of features, particularly including the distinctive vestiture of glandular trichomes with extremely long stipes. And in spite of its white rays, it fits more securely in that genus than in *Aster*, particularly when it is placed next to *T. aberrans*. This view of the taxonomic placement of *A. kingii* is reflected in the following two nomenclatural combinations:

Tonestus kingii (D.C. Eaton) Nesom, *comb. nov.* BASIONYM: *Aster kingii* D.C. Eaton, *Bot. Fortieth Parallel* 5:141. 1871. *Machaeranthera kingii* (D.C. Eaton) Cronquist & Keck, Brittonia 9:239. 1957.

Tonestus kingii (D.C. Eaton) Nesom var. **barnebyana** (Welsh & Goodrich) Nesom, *comb. nov.* BASIONYM: *Machaeranthera kingii* (D.C. Eaton) Cronquist & Keck var. *barnebyana* Welsh & Goodrich, Brittonia 33:299. 1981. *Aster kingii* D.C. Eaton var. *barnebyana* (Welsh & Goodrich) Welsh, Great Basin Naturalist 43:221. 1983.

Var. *barnebyana* is weakly distinguished, but it is restricted to the southwestern corner of the range of the species, and as noted in its original description, its leaves are characteristically toothed and the biseriate glands are longer than in the typical variety. In these features, var. *barnebyana* is more similar than var. *kingii* to related species within *Tonestus*.

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